PHYLOGENETIC IMPORTANCE OF THE XYLOTOMY AND GEOGRAPHICAL DISTRIBUTION OF HOMOXYLIC DRIMYS WINTERI AND DRIMYS COLORATA (2)

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Abstract

In the Introduction, the author gives a short survey of the xylotomic investigations into the homoxylic trees. He deals in details with pitting of the tracheids of homoxylic trees, more exactly of *Drimys winteri* and *Drimys colorata,* with the origin of the spiral and stepped thickening, with the phylogenetic importance of monoecism, dioecism, and of the hermaphroditic (bisexual) states. In ultimate analysis, he arrives at the conclusion that Drimyses and their relations (Tetracentron, Trochodendron), as anciant types, cannot have originated — on the basis of their xylotomic, phytogeographic and genetic particularity — from Magnoliales (sensu TAKHTADJAN). Probable, they — as vesselless plants of aggregated pith ray, of various sex, with amenta, tracheids — are genetically rather closer to the vesselles homoxylic Conifers and Amentiflorae of varying sex with amenta than to Magnoliales (sensu TAKHTADJAN) of more developed vessels and hermaphroditic flowers, functioning with a torus.

Introduction

The first phylogenetic monograph of the author „Ein Gedanke zur polyphyletischen Entwicklung der Pflanzenwelt", was published during World War I, in 1918 (cf.: References). Here he first proclaimed the doctrine of phylogeny of land plants in three directions, from the state of protophytes till the most developed plants, i.e. the angiosperms, including the origin of monocotyledons and dicotyledons, as well. Later on, an animated discussion was carried on in this field, particularly in connection with the homoxylic trees. Concerning this, in Metcalfe's book the following are to be read:

Bailey and Nast in their study of the morphology of this group have shown that, with the exclusion of *Illicium*, the Winteraceae become a homogeneous, natural aggregation of obviously closely related plants. Within the group, these authors distinguish the following trends of structural specialization: "toward reduction or elimination of wood parenchyma in Sect. *Wintera* of *Drimys*, toward excessively widened multiseeiate rays in *Pseudowintera*, and toward reduction of cell size, particularly in dwarfed or microphyllous species e.g. in Sect. Tasmannia of *Drimys*."

The occasional scaliform pitting that occurs in the tracheids of *Drimys*, figured largely in the controversy of about 1918, assiciated with the names of BAILEY and JEFFREY, as to whether *Drimys, Tetracentron,* and *Trochodendron* represent degenerate evascularized Dicotyledons, the ancestors of which possessed true vessels in their secondary xylem, or whether they have descended directly from ancestors that possessed scalariform tracheids in their secondary xylem. Modern work on the significance of the length of the cambial initial and vessel members has provided a means of testing such hypotheses and BAILEY and NAST, in 1945 stated that the primitive character of the cambium and xylem in the Winteraceae, *Trochodendron* and *Tetracentron* rules out any possibilities of these plants having developed vessels and subsequently having lost them. Elsewhere they claim that, when evidences

from all organs and parts of the plants are taken into consideration, there are no convincing arguments for deriving the Trochodencraceae from the Winteraceae or vica versa, or even for inferring that these families are closely related genetically. Nor con one assume that the other ranalian families were derived from these vesselless and the Coniferae overlook important anatomical differences, such as occur in the rays, and are thus misleading. They conclude that if the vesselless wood of the Winteraceae is to be compared with that of the Gymnosperms, it should be with the secondary xylem of Pteridospermae and Bennettitales rather than with that of the Coniferae, Ginkgoales or Cordaitales."

TAKHTADJAN's booklet of the origin of Angiosperms was published in Russian 1954, which he sent to the author of this paper as well. This book is of 96 pages extent, containing 16 illustrations. The 16th of these is showing a phylogenetic table, tracing the origin of angiosperms back to a single common stock, the Magnoliales. With this, he considers the origin of angiosperms as monophyletic. This theory is diamatrically opposed to the above theory of the author. In the meantime, other authors have also dealt with this problem, particularly with the peculiar structure and taxonomic position of homoxylic trees (ZIMMERMANN, LAM, ASAMA, etc.). Some of them consider particularly the homoxylic trees as degenerate forms: others are, however, adherents of the polyphyletic conception.

In 1954, the author presented his theory in Paris, in the International Botanical Congress, as well. In 1962, he dealt with this problem, again, making use of the recent literary data. The title of this monograph was: "The phylogeny of sexuality and triphyletic evolution of land plants". In this work, he repeats his older opinion, regarding the origin of land plants.

TAKHTADJAN's work, entitled "Evolution und Ausbreitung der Blütenpflanzen" was published in 1975. His phylogenetic theory has been published here repeatedly. In the mean time, his theory was reviewed, and partly even accepted, in more than one country. Thus, among others, the Hungarian professor REZSŐ SOÓ has entirely taken over TAKHTADJAN's system in his university textbook (Phylogenetical phytotaxonomy). And even, in the University Botanical Gardens in Szeged, ENGLER's system was transformed and replaced by TAKHTADJAN's system.

In the meantime, however, this system has been criticized by several authors. Thus, among others, by Gottwald in Hamburg. He proves on a very wide xylotomic basis that Magnoliales cannot be the ancient angiospermic type because there are some plant families and orders, too, carrying much younger characters. In his paper, he writes: "Abstract". The stem wood of about 700 species, belonging to 32 families of the order Magnoliales s.l., plus further taxa exhibiting primitive wood anatomical features were investigated. On this basis, six structural groups can be established each of which shows a marked gradation from primitive to advanced stages. Wood structure of Magnoliales sensu TAKHTADJAN is only partially primitive, partially moderately derived, while the most primitively structured heteroxylous taxa belong to the "Dillenial-Hamamelidal" and "Theal" groups, respectively. Accordingly, there is no compelling evidence to support phylogenetic schemes in which the Magnoliales is placed as the only common base for all recent dicotyledons."

The authors has got the opportunity in 1979, to procure some wood of homoxylic *Drimys* winteri and to investigate into it from xylotomic point of view. He renders account of the results of his investigations in the following way.

"The author considers, contrary to TAKHTADJAN's theory of monophyletic origin, that a polyphyletic origin of the angiosperms is more probable and he wants

to support his opinion by xylotomy of the homoxylous *Drimys*, comparing it with a *Juniperus* and a *Magnolia*. As *Drimys* has only tracheids with simple pits and is without vessels, while in the Magnoliales vessels occur, and as the tracheic state is mor primitive than the vessel-containing one, the homoxylous trees could, therefore, not originate from Magnoliales".

Materials and Elaboration

In the following, we attempt to verify that Drimyses *(Drimys winteri, Drimys colorata)* cannot originate from the order Magnoliales, as supposed by the Soviet TAKHTADJAN and his followers, e.g. the Hungarian Soó. We will support our statements with photographs and arguments.

We will prove, why the origin of angiosperms cannot be monophyletic but only polyphyletic, why Magnoliales cannot be the prototype, from which all the mono- and dicotyledons, the monoecious and dioecious plants would have come (Plate I).

In Plate I, there are six photographs. They are showing the species of: 1) a gymnospermous tree *(Amentotaxus argotaenia)*, 2) and 4) the homoxylous *Drimys winteri*, 3) *Drimys colorata*, 5) *Alnus incana* (Amentiflorae), 6) Magnolia accuminata (Dialipetalae). The cross-section structures of the gymnospermous pine and of the two Drimyses (2 and 4) are very similar to one another. Vessels are missing in both. The whole stock consists of tracheids. Fig. 1. is showing the cross-section structure of *Amentotaxus argotaenia*. In the one cell-layer, elements of two sizes are arranged, between wide pith rays. The elements generally follow one another in radial direction. Between them, in a smaller or larger distance, there were generally arranged larger tracheids of regular cylinder-form and then smaller ones of angular cross-section. Tracheids of two different sizes seem to have developed already here, in pines; and from the larger ones may have been formed the later real tracheids and vessels, and from the smaller ones the parenchyma cells.

It is interesting that inside the wider tracheids spiral thicknesses lie. These vessels are, however, missing from the gymnospermous pine, the Drimyses. In this regard, Drimyses are closer to gymnosperms than to Magnoliales. It is interesting, too, that in both Drimyses aggregated pith rays also occur but these are missing from pines and Magnoliae.

In Figs. 2 and 4, there are two kinds of cell of cell types near to each other. In Fig. 4, this can be established well. The capital letters show the tracheids, while the cyphers rather the parenchymatic cells, radially somewhat elongated. In Fig. 5, about Amentiflorae *Alnus glutinosa*, the part of a pith ray is to be seen, where the tracheid series alternate with the mono-layer parenchyma. A fully identical structure is visible in the homoxylic *Drimys winteri*, as well (Fig. 4). On the other hand in Fig. 6, in the *Magnolia*, and also in its other relations, there do not occur any aggregated pith rays.

On the basis of the presence or the lack of the aggregated pith rays, Drimyses can rather be brought into a nearer genetic connection with Amentiflorae than with the Magnolis, belonging into the the Dialeptale. As such an ancient feature is entirely missing from Magnoliales, but they are to be found in Drimyses and Amentiflorae, they may therefore not have origined from Magnoliales, as imagined by TAKHTADJAN and his followers. For proving that this is an ancient feature and that it, as such one, has nevertheless remained, we enumerate here a number of such Amentiflora species: *Casuarina aequisetifolia, Alnus incana,* (Fig. 5) *Alnus glutinosa, Corylus avellana, Fagus sylvatica, Fagus orientalis, Quercus cerris, Quercus ilex, Quercus petrea, Quercus robur, Quercus borealis maxima, Carpinus betulus,* and even Ephedrae, etc., etc. Such aggregated pith rays cannot be found at all among the monocotyledonous trees — these having otherwise no pith rays — and occur among the dicotyledons, too, only in the rarest cases. It is proved — therefore, already on the basis of cross-sections that the development of angiosperms did not set out from Magnoliales. Before these were already the primitive homoxylic trees, the structure of which already reveals more details.

Pitting of the wood of Drimys winteri and Drimys colorata

The xylem of Drimyses is formed — as seen before — by large and only by tracheids and scanty parenchyma cells. A characteristic property of tracheids is that they are unicellular, in their walls only simple pits line up. In Fig. 7, the simple

Plate I

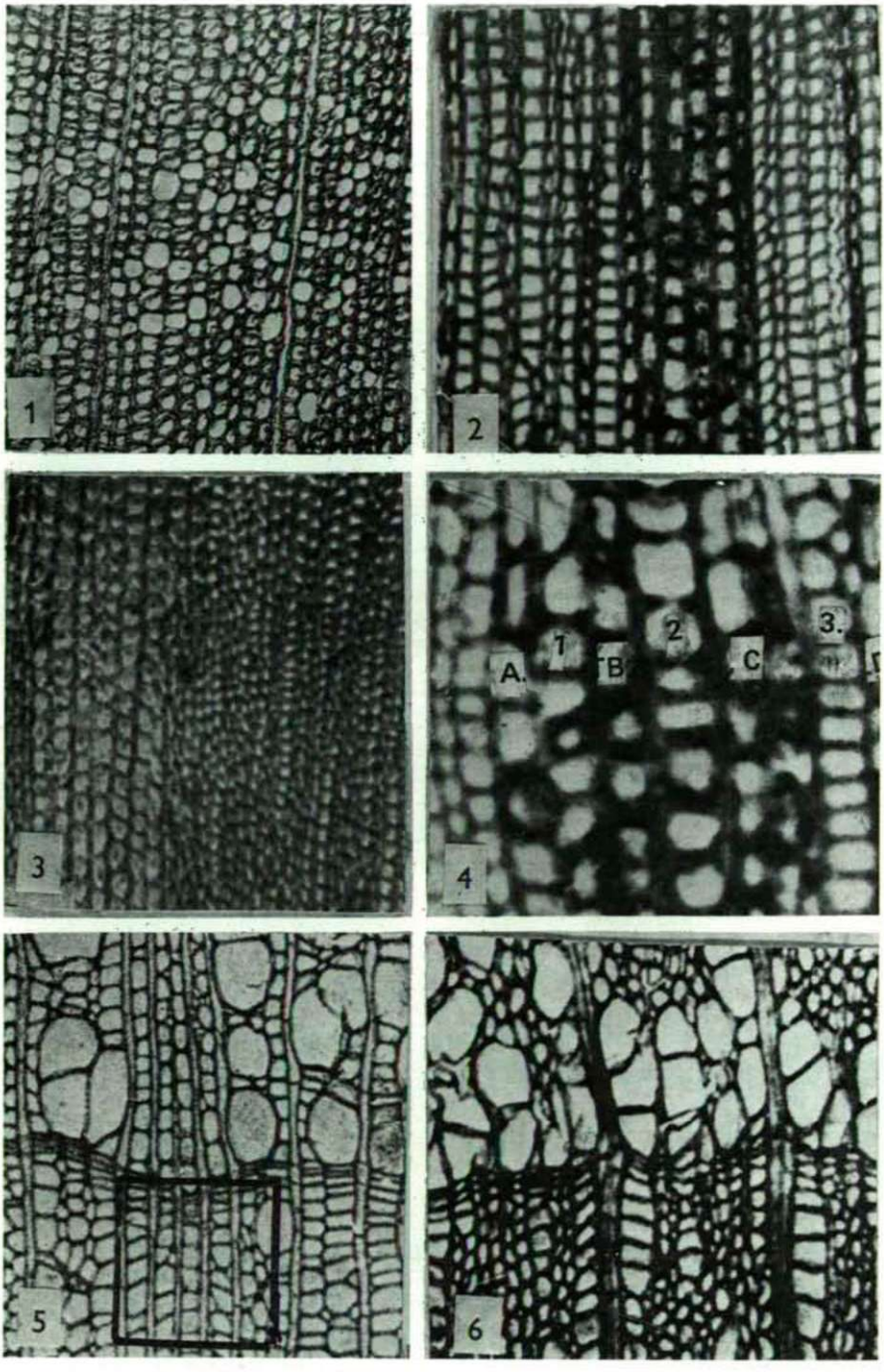
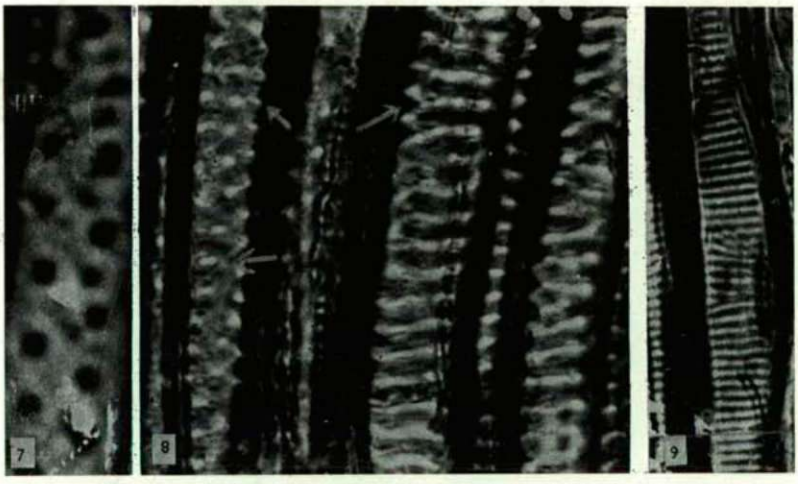


Plate I

1. Cross-sectional picture from the trunk of the gymnospermous pine *Amentotaxus argotaenia.* The cross sections of the two kinds of elements are separated well from each other. The major ones are tracheids, the minor ones are parenchyma cells, arranged in radial lines. The pith rays are singlelayer. This structure is rather similar to the *Drimys* than to Magnoliales (x100).
2. Cross-sectional structure of the homoxylic *Drimys winteri.* In the middle is running, separated, an aggregated pith ray. The matter of the xylem also consists of tracheids. Their cross-sectional structure is generally square, here as well. In their size they differ a little from the somewhat smaller rows, which probably are unicellular pith rays or parenchyma rows. This structure is more similar to that of Amentotaxus than to that of Magnoliales (x100).
3. Cross-sectional structure of *Drimys colorata.* On the left an aggregated pith ray is lying, separated by its major cells. The matter of xylem consists, here too, of tracheids. Vessels are entirely missing (x80).
4. Magnification of a detail of picture 2. The capital letters indicate the radially elongated parenchyma rows, while by ciphers the tracheid rows between these are indicated (x180).
5. Cross-sectional structure of the dicotyledonous Amentiflorae *Alnus incana.* In the ground tissue of the tracheid, between the parenchyma cells and the cornered tracheids, solitary twin poles and pore rays take place. In the black square, there is a detail of an aggregated pith ray (x200).
6. Cross-sectional structure of *Magnolia accuminata,* ranged into Dialipetaleae. In the xylem tracheids, single vessels, pore rays, and pith-ray cells take place. There are no aggregated pith rays. (x200).

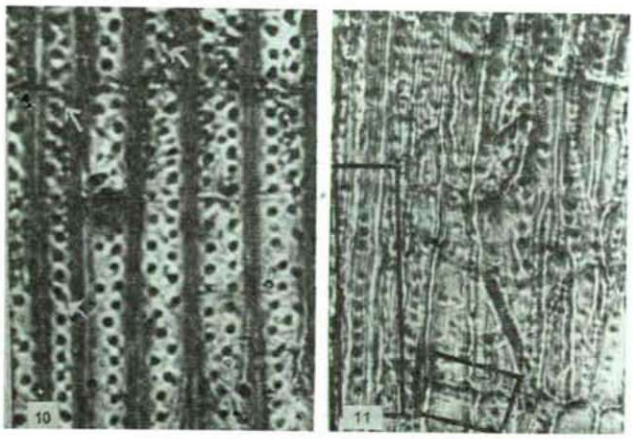
Plate I



7. Tracheid structure from *Drimys winteri.* In the wall of tracheids, the simple pits are arranged separatly and in alternating lines. There are no bordered pits (x150).
8. In the walls of eraly tracheids, the simple pits take place in pairs or in threes, spirally and in slanting rows. The pits are open or compact (see, on the left, at the white arrow). In the middle, the openings of pits take place spirally. These are not step-ladders, like those to be seen in Magnoliales. There is an essential difference between the two. Stepped thickness occurs only in Magnoliales. In Drimyses it doesn't (x150). occure.
9. Stepped thickness in Magnolia accuminata. In Drimyses, the edges of spirals are uneven, while in Magnoliae the steps of the stepped thickness are parallel and straight (x125).

pits are wellvisible, following one another alternatively. Another property of pittings is "oppositions", when the pits follows one another in horizontal or longitudinal lines. In Drimyses, no pits like this occur. It is interesting that in the walls of tracheids

Plate I



10. Six tracheids from the ray-side of *Drimys winteri*. In the walls of tracheids, the simple pits are arranged in 1 to 2 lines. (x175).
11. Radial side in the tracheids of *Drimys colorata*. In the framed rectangles there are thin-walled parenchyma cells, with single-line large, simple pits in their walls. (x160).

the simple pits are always located in a certain definite distance from each other. At the first glance, these regular circular openings are surrounded by light boundles and they look to us as if the micelles (?), forming the part of the wall, had been arranged in a sequence. In Figs 10 and 11 can be observed well enough.

Observing this, it seems to us as if the central pi were always be surrounded by two spiral plexuses, each. In Fig. 16 to the left from the cipher, we see such details. The two bundles, running in opposite directions, lie one above the other with lateral pits in them. Consequently, the tracheids form a tube-like system. The tube-like structures are to be seen very well in Fig. 16 in the part at the small cipher 2.

The situation will be still more complicated, when in the wall of the tracheids not only one but even two or three pits can take place, in an alternating position with the foveolae below them. All these are visible on the left of Fig. 8, where below one, and above it, two or three pits lie close together and apparently a ladder-like thickening comes into being. This is, however, no right observation because the simple pits being in an alternating situation, touching with one another, seem to be

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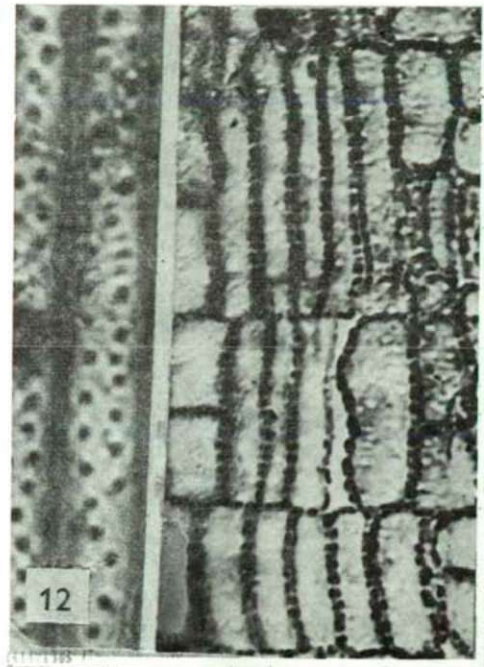
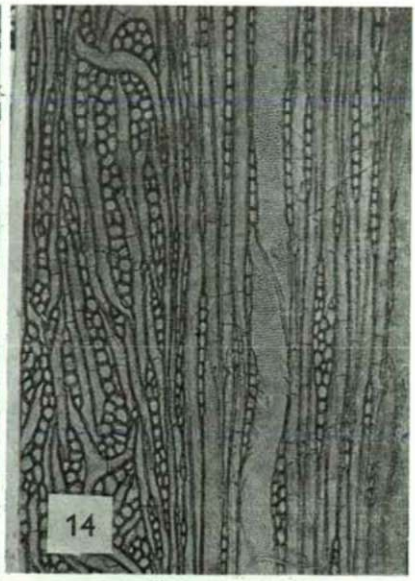
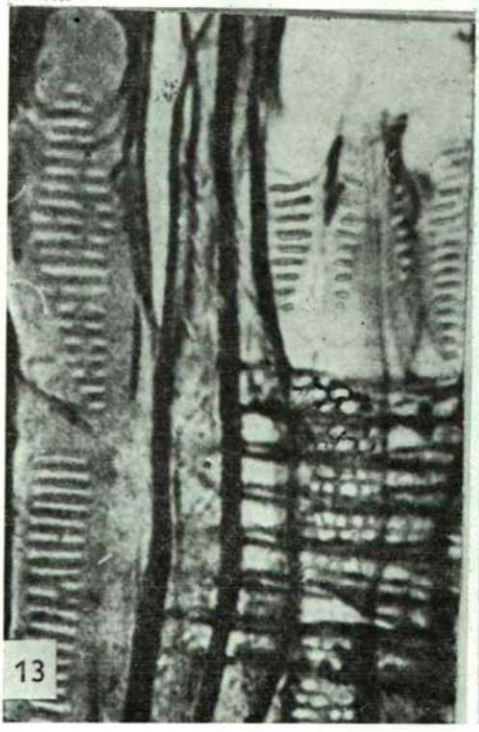
Plate I

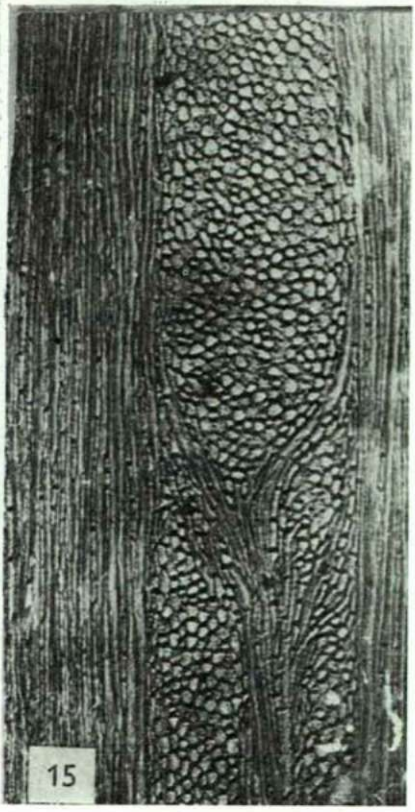
12. On the left, there are two elongated tracheids with simple pits. The same pitting is shown by the cells of the wide pith rays. On the right of the picture, a tracheid formulation is to be seen. The pith-ray cells are initially cube-like, divided vertically, becoming 4-cellular and, at last, longitudinal tracheids (x120).
13. Radial structure from *Magnolia accuminata*. On the left, there is a stepped vessel, above a simple perforation. On the right below, they are horizontally elongated. In the walls, touching the vessels, there are simple, round pits. This is also a difference between two kinds of pith rays (x120).
14. An aggregated pith ray from Amentiflorae *Alnus incana*, composed by more than one, one- or two-layer, smaller pith rays (x110).
15. An aggregated pith ray from *Drimys colorata*. (Tangential side). Tracheid basic substance and pith-ray rows (x110).

Plate I





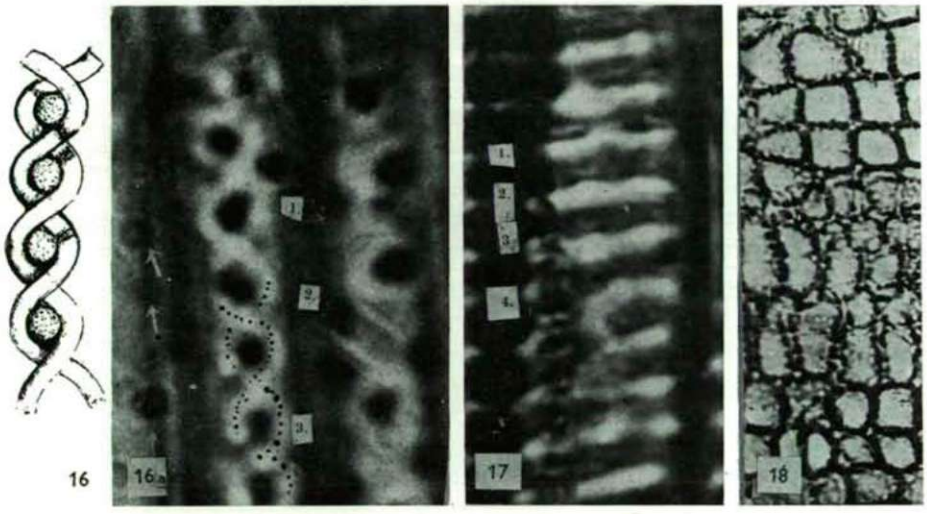




distinguishable counter-laths. For a perfunctory observation this seems to be a ladder-like thickening, whereas these are, in fact, spiral formations. The most interesting in these formations is that they are of tubular structure, they seem, therefore, to have inside small cavities. In Fig. 17 at the tiny ciphers, the tubules are torn, showing the tubular structure clearly.

This spiral structure essentially differs from the ladder-like thickening of Magnoliales (Fig. 9). Drimyses cannot have originated from Magnoliales, if only on the ground that the spiral structure is formed in another way than the ladder-like thickening. The explanation of that is in tracheids, these horizontal tubules seem to be step-ladders, the spiral lines are running in these paces cery close to one another. This is a tubular structure, something which could not be observed, so far, either in pines or in deciduous trees. It is proved by different anatomical structures, as well, that Drimyses cannot have originated from Magnoliales because their wood anantomies are essentially different from each other. (Cf. GOTTWALD.) That these spirals are tubules, it is proved by the circumstance, too, that in certain places tubules seem to be obstructed. This can be seen very well at the lower white arrow of Fig. 16, resp. to the left from cipher 16, at the edge. The ruptures can be observed well at the small ciphers 1, 2, 3, 4, 5, 6 of Fig. 17. At cipher 2, the cavities are to be seen at the ends of the two half-rings. Both ends of the crescent-like piece, No. 2. are torn, reminding us of a cross-cut ring.

Plate I



16. Simple pits in the walls of tracheids. On the left, at the arrow, there are simple pit-openings. At cipher 16 (in the corner), the cavity, thin wall of the tracheid is to be seen well. The dotted line (in the middle) is indicating the formation of two contrary bundles. At the small cipher 1, it is visible well enough, as the two bundles interwined surround, resp. form the simple pit. At the small cipher 2, the cavity and wall of the tubule is well-observable (x190).

16a. Formation of simple pits in the walls of the tracheid of Drimys winteri.

17. At the small sciphers, the tube-like openings of the cross-thicknesses are to be seen, indicating that these Thicknesses are of tubular and spiral structure (x190).

18. In the wide aggregated pith rays, the cube-shaped parenchyma cells are simply pitted, like those of tracheids (x75).

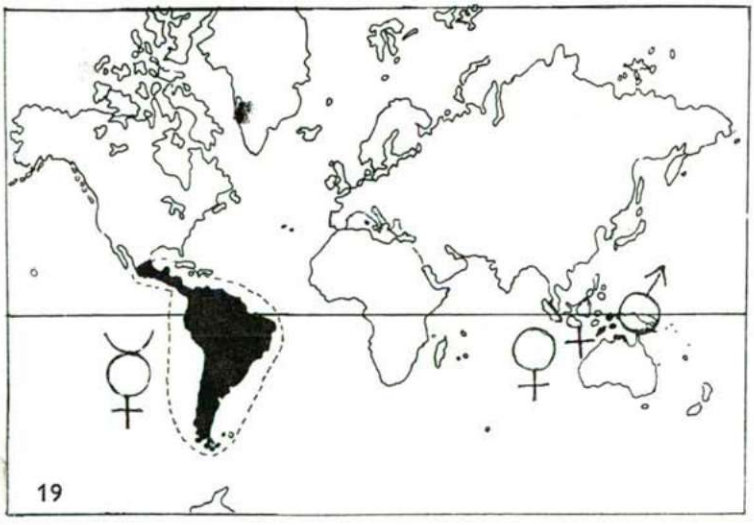
Another matter surprising fact is also shown by the structure of pith rays. Fig. 8, as mentioned, in Drimyses, some pith rays develop, as well; generally, they are one cell layer or 15–20 cells wide, and generally of heterogenious nature. In Fig. 12, the marginal cells of the wide pith rays are of different length. Initially they are one, then two, later on four cells long and become high tracheids. The inner cells are, however, rather isodiametric and simply pitted. On the other hand, however, rather isodiametric and simply pitted. On the other hand, the cells of pith rays of Magnoliae (Fig. 13) and generally of the higher woody.

The geographical distribution of Drimyses

The vesselless Drimyses belong to the similarly vesselless Winteraceae family. Concerning this, we can read in METCALF's book the following: "A family of trees and shrubs, occurring chiefly in certain parts of South-East Asia and South America. *Drimys* is the only genus which occurs in both the Old and New Worlds. Smith, who has recently revised the taxonomy of the family, points out that the american species are all hermaphrodites, whereas those from the Old World are dioecious (Fig. 19).

On the other hand, in ENGLER–PRANKL's paper we can already read some data in detail: "*Drimys*, Bl., zwitterig, polygam oder diklin. Ungefähr 40 Arten, davon *D. Winteri* Forst in verschiedenen Varieteten von Mexico bis zur Magellan-Strasse in den Gebirgen und höher gelegenen Gegenden, 4 Arten in Australien, 2 in Neuseeland, je 1 in Neukaledonien, Neuguinea und Borneo (Fig. 19).

But what is the connection between the geographical distribution of Drimyses, xylotomy, and the distribution of their genera? Seemingly nothing. But essentially, we can draw far-reaching conclusions from the connection of these. In order to



19. The geographical distribution of the homoxylic Drimyses. They are hermaphroditic in the whole South America (ca. 35 species), while in South-East Asia, in one or two islands, only four-five dioecious species live.

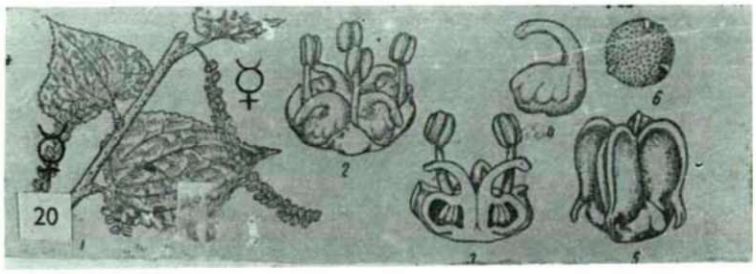


Fig. 20. The hermaphroditic amentiflorae, flower, fruit, seed, and pollen grains of *Tetracentron sinense*.

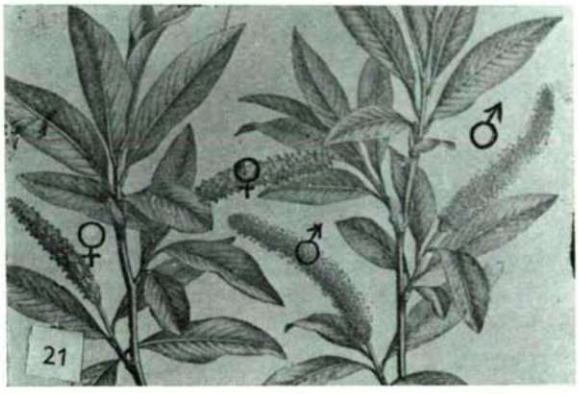


Fig. 21. The staminate and pistillate unisexual amentiflorae of the dioecious *Salix*.

understand the following, we have to mention certain basic laws of genetics. Which are these? Every living being, be it animal or plant, monocellular or gigantic, has some sex. It is, therefore, either male or female. Or, it may be hermaphroditic. To this rule, there is no exception. Thus, it concerns trees, i.e. homoxylic Drimyses, as well. Drimyses are landplants. Each individual develops from a seed. The seed, however, already contains the sexual character, as well. From one seed, only a male, i.e. a polliniferous individual develops. The plant itself is dioecious, i.e. amphibious, because the progeny, i.e. the seed needs two kinds of parents to its formation. These are the so-called homospermatic plants (Fig. 21). From the other kind of seeds, independently of its size, an individual develops, in which the two kinds of multiplying organs get nearer to each other. Thus, the creation of progeny becomes surer. In these, in certain shoots, polliniferous flowers (catkins) develop, while in other shoots female flowers. Pollination is uncertain enough in both cases because it takes place by the mediation of the wind. At any rate, this seems to be more advantageous from the point of view of the progeny than the dioecious state is.

The third type of seeds is, when from the same kind of seeds the same kinds of individuals develop. These are the most highly developed seedy land plants, angiosperms. Pollination takes here already place generally by the mediation of insects. The hermaphroditic state is therefore, more developed, though younger, than monoecism or dioecism. In the course of phylogeny, as well, the dioecious

plants with changing sex and the monoecious ones, thus Coniferae, Cycadaceae, frc., etc. appeared as first from among the high-growing plants. It is interesting that teom among the Pine families (Taxodiaceae) are rather monoecious north of the Equator, while the dioecious ones, thus Araucariaceae, Podocarpaceae, Taxaceae, Cycadaceae are mainly distributed in the southern globe.

Applying this law of nature to Drimyses, as well, among which there are both liroecious and monoecious ones and hermaphrodites, we see that among these, the dehmaphrodites are the youngest, and the dioecious ones the most ancient, i.e. the odest ones. TAKHTADJAN regards the youngest type, i.e. the Magnoliales with hermaphroditic flowers as the first in the formation of angiosperms. In our opinion, this is erroneous. For proving this, we only mention the following. Those with hermaphroditic flowers the ancient ones, then how can they arrive at the state of separated sex, dioecism? In this case, those with hermaphroditic flowers should develop instead of one seed pollen resp. individual. (Two seeds, with the organs of propagation in them, in order to develop of them healthy progeny. But this would be connected with an enormous waste of material. They would have to renounce the surer pollination by insects and choose the uncertain pollination by wind, etc., etc. Such a possibility has so far not occurred, as yet. 2) And if we consider dioecism as more ancient — as we do — we could renounce the creation of the other animal. This would, at any rate, mean economy of materials, too, but these would get, instead of the uncertain pollulation by wind, into the state of the much more certain pollulation by insects. This has followed in South America and South-East Asia, when the hermaphroditic *Drimys* species (the South-Americans in 85 p.c.) overran the latter continent, while the four to five dioecious species, having survivd ine South-East-Asia are dying out, showing that dioecism is the more ancient, older, and the hermaphroditic state the younger, more succesful and advantageous, as well.

The hermaphroditic state rather promotes the greater and faster distribution. At propagation, the hermaphroditic state and monoecism need only one, dioecism always two kinds of seeds, that is to say, two times so many. The double amount of seeds needs a double area. Therefore, distribution also needs a larger territory. Thus, it is handicapped to the monoecious and hermaphroditic individuals. And in the struggle for life, this is a very important circumstance.

The dioecious plants are, therefore, fully and necessarily pushed into the background by the hermaphroditic state, as a consequence of which the dioecious plants become more and more exhausted and perish. In the course of phylogeny, too, in the various geological ages, the species prevailed, the reproductive organs, resp. the gametes of which have got as close to one another, in space and time, as it was possible.

In the opinion of the author, it is not only improbable but even impossible, to originate the dioecism from the hermaphroditic flowers of angiosperms, because it would be opposite to evolution. The inversed process is natural. The unisexual flowers are more ancient and the bisexual ones are younger, this is verified by the palaeontological and pollenanalytical data, as well as by the enclosed Plates, too.

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